Colonisation in New Zealand streams: predictable patterns or chance events?

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Abstract

The question of whether new habitats are colonised by a predictable sequence of species has been central to understanding how communities in both aquatic and terrestrial systems are formed. Despite considerable debate the question remains unanswered although traits that characterise species as good colonisers are often associated with many taxa. The examination of data from three colonisation studies in New Zealand indicates greater community similarity within streams, irrespective of colonisation time, than between streams colonised for the same length of time. These studies provided no evidence for the presence of a suite of common taxa, which colonise new substrata but are later replaced by more strongly competitive taxa. Colonisation of newly disturbed patches of substrate by invertebrates in the study streams appeared to be by crawling and drifting from the surrounding streambed rather than through a predictable sequence of arrivals of specialised colonists.

Keywords: colonisation - Canterbury - disturbance - stream invertebrates - Urewera - Whatawhata.

Introduction

Physical disturbance by increased flow is one of the dominant forces controlling stream invertebrate communities (Resh *et al.* 1988; Lake 2000; Death & Zimmermann 2005). Disturbance removes habitat, individuals and their food resources, which include periphyton and particulate organic matter. Despite often frequent disturbance events many stream invertebrate communities remain remarkably constant over time (Townsend *et al.* 1987; Holomuzki & Biggs 2000; Scarsbrook 2002). Thus, although floods often lead to reduced density and diversity of invertebrates (Scrimgeour *et al.* 1988; Collier & Quinn 2003) communities recover from those disturbances relatively quickly (Boulton *et al.* 1988; Death 1996; Matthaei *et al.* 2000), and appear to be the result of high abundances of drifting invertebrates typically present in the water column (Brittain & Eikeland 1988; Downes & Keough 1998). However, although the effects of flood disturbance are well established the process of colonisation

after disturbances is considerably less well understood (Downes *et al.* 2005).

Ecological theory postulates that a suite of specialist taxa will colonise immediately after a disturbance and subsequently will be replaced in a successional sequence by later arriving, but competitively dominant taxa (Begon *et al.* 1990; Roxburgh *et al.* 2004; Shea *et al.* 2004). Several models, such as the intermediate disturbance hypothesis and the dynamic equilibrium hypothesis rest on a trade-off between taxa being good at colonising and being strong competitors (Chesson & Huntly 1997; Roxburgh *et al.* 2004). Similarly, ideas of succession and assembly rules rely on some taxa arriving early following a disturbance and others arriving later and replacing those early colonists (Weiher & Keddy 1999). Several authors have identified stream invertebrate taxa or life history traits that are often associated with strong colonising ability (Mackay 1992; Poff 1997; Townsend *et al.* 1997), although identification of the postulated trade-off between competitive and colonising ability in stream invertebrates has been more contentious (Reice 1985; Death & Winterbourn 1995; Death 1996).

Most colonisation studies have been undertaken in a single stream (e.g., Doeg *et al.* 1989; Douglas & Lake 1994; Downes *et al.* 1998; Loo *et al.* 2002) and therefore have not considered whether a common core of specialised colonising taxa is found in different streams within a region. In this study I examine patterns of colonisation in three New Zealand studies that each included multiple streams in an attempt to identify whether a suite of taxa could be characterised as specialised colonists and whether they are replaced by later-colonising, competitive dominants. The first study examined the effects of disturbance and colonisation in baskets of cobbles placed in four Canterbury high country streams (Death 1996). The second study examined colonisation of clay tiles placed in three pasture streams at Whatawhata near Hamilton (Guy 1997). The final study examined colonisation of clay bricks in six forest streams in Te Urewera National Park (R.G. Death unpublished data).

Scale is always an important consideration when conducting ecological studies and experiments (Parsons *et al.* 2004; Townsend *et al.* 2004), and in all three studies the focus was on disturbances at the patch scale not that of the reach or stream. Results of similar studies at these larger scales may therefore differ considerably from those considered here as colonisation processes will be influenced by different factors, for example availability of egg-laying adult insects. However, the scale of the three New Zealand studies is that at which many disturbances, such as spates affect stream beds and their associated biota (Lancaster & Hildrew 1993; Death 1996; Matthaei *et al.* 1999).

Materials and Methods

Canterbury

The experiment was conducted between 4 February and 8 April 1989 in four streams (Kowai River, Whitewater Stream, Porter River and Grasmere Stream). Wire mesh baskets (30 x 15 x 10 cm) with 1.25 cm mesh sides were filled completely with clean stones from the upper banks of nearby streams. Five large stones (longest diameter 7-10 cm), and cobbles 2-6 cm diameter were placed in each basket. Twelve baskets were buried in the streambeds at each site in a stratified random manner (i.e., the three treatments

were placed randomly across the stream) with their rims level with the surrounding bed surface.

A third of the baskets (i.e., four per stream) were disturbed each week for nine consecutive weeks. This was done by lifting a basket from the bed (but not out of the stream), shaking it vigorously for 30 seconds, and then replacing it. Another four baskets in each stream were given this treatment every third week for nine weeks, and the remaining baskets were left undisturbed. At the end of the nine-week period, all baskets were lifted into a net (250 µm mesh) held immediately downstream, preserved in formalin and returned to the laboratory.

In the laboratory, cobbles were washed and removed from the remainder of each sample. Organic material, including invertebrates in samples from Kowai River and Whitewater Stream were then separated by floatation in a saturated solution of $CaCl_2$, and the remaining fine inorganic sediment was searched for cased caddisflies and molluscs. Floatation was not used for processing samples from the other two streams which lacked large amounts of fine inorganic sediment. All animals were identified to species level where possible using available keys and counted (Winterbourn & Gregson 1989). If taxa could not be named, they were differentiated into apparent morphospecies. Counts of animals with densities greater than 200 per sample were made after sub-sampling with a bipartite sub-sampler. More details of the study including the collection and analyses of physico-chemical data can be found in Death (1996).

Whatawhata

Twenty terracotta tiles (Revestimentos Ceramics, Apartado Aereo 27540, Bogota, Colombia) were placed in five rows of four in riffles within three pasture streams. The tiles measured 21 x 11 x 1 cm (0.05 m^2) and were secured by looping a strap of motorcycle tyre inner tube around each tile and wiring them to pegs driven into the stream bed.

All tiles were placed in the streams on 25 or 27 January 1996. Four randomly selected tiles were removed from each stream into a 250 µm-mesh net after 1, 4, 7, 21 and 42 days, the trial concluding on 7 or 9 March 1996. Invertebrates were brushed from tiles and preserved in 70% isopropyl alcohol. Macroinvertebrates were identified or assigned to morphospecies and enumerated as above. More details of the study including the collection and analyses of physico-chemical data can be found in Guy (1997).

Urewera

Experimental substrata were Monier® clay pavers 23 x 11 x 5 cm and had similar surface texture to natural stream stones. Half of the bricks had four equidistant grooves (11 x 1 x 1 cm) cut in their upper surface. The equivalent surface area created by the grooves was removed from these tiles by reducing their length.

Bricks were placed in the streams in pairs (one grooved and one without grooves) along a 50 m stretch of each stream in February 1998. Five, randomly selected pairs, were collected 3 days, 1 week, 4 weeks, 8 weeks and 15 weeks later. Bricks were lifted into a 250 µm-mesh net held directly downstream and their top and bottom surfaces were scrubbed with a nylon brush. Collected invertebrates were preserved in 10% formalin and later identified and enumerated to the lowest possible taxonomic level using the keys of Winterbourn (2000) and Winterbourn *et*

al. (2000). Fauna from grooved and non-grooved bricks were identical (Death ms) and therefore were pooled for all analyses. More details of the study including the collection and analyses of physico-chemical data can be found in Death (ms).

Data analyses

To compare habitat conditions at sites within a study Bray-Curtis similarity measures were calculated for physiochemical measures recorded at the study sites. Data were normalised prior to calculation so that each measured variable was assessed on the same numeric scale.

To compare stream faunas, Bray-Curtis similarity measures were calculated from presence/absence data for baskets, tiles and bricks collected at the end of each study. The concurrent occurrence of common taxa (those comprising 5% or more of the fauna at any time during the study) at all sites within a study was also examined in the same way but using mean relative abundance data.

Patterns of community composition during colonisation were examined with non metric multidimensional scaling (NMDS) on log (x+1) transformed relative abundance data using Primer (Clarke & Warwick 1994). Changes in density for abundant taxa (those comprising more than 15% of the fauna in any collection) with time for colonisation were analysed in SAS (SAS 2000) using a two-way analysis of variance. Site and Time were treated as fixed factors. Type-4 sums of squares were used because in a few cases not all replicate experimental units were recovered. Densities were log (x+1) transformed prior to analysis to remove heteroscedasticity.

Results

Stream characteristics

Canterbury

The streams and rivers used for the colonisation study in Canterbury were in the Southern Alps between Porters Pass and Cass, and drained predominantly tussock vegetation. The streams were of moderate size, 1st- to 3rd- order, with mean annual depth and current velocity in midstream ranging from 16-24 cm and 0.46-0.8 m s^{-1}, respectively (Table 1). All sites had similar substrata (Substratum size index 6-9), moderately hard water (17.6-33.2 mg l^{-1} $CaCO_3$), near-neutral pH (7.4-7.7) and low nutrient concentrations (NO_3-N <0.05 mg l^{-1}, reactive PO_4-P <0.004 mg l^{-1}). Two of the streams were designated unstable (Kowai River and Whitewater Stream) and two stable (Porter River and Grasmere Stream) based on a number of hydrological and thermal measurements made between December 1987 and May 1989 (Death & Winterbourn 1994). Habitat characteristics measured at the sites during the experiment are presented in Table 1. Multivariate Bray-Curtis similarity between the sites based on the physico-chemical measures above ranged from 88 to 96%.

Whatawhata

The three streams in the Whatawhata study were located in hill country pasture. The streams were small, less than 2 m wide, with a depth between 5 and 7 cm during the study (Table 1). Substrata were silt and gravel with a few larger cobbles. Conductivity and water temperature were relatively high and reflected their drainage of pasture used to graze cattle and sheep. Multivariate Bray-Cutis similarity

Table 1. Mean habitat characteristics measured at the streams during the colonisation studies in Canterbury (February - April 1989), Whatawhata (January - March 1996), and Te Urewera National Park (February - June 1998). For details of methods used, see Death (1996); Guy (1997); Death (ms). Substratum size index is calculated following Quinn & Hickey (1990).

Sites	Stream Order	Substratum size index	Canopy cover (%)	Riparian forest vegetation (%)	Channel width (m)	Depth (cm)	Velocity ($m\ s^{-1}$)	pH	Conductivity ($\mu s\ cm^{-1}$)	Temperature (°C)
Canterbury										
Kowai	2	8	0	0	5.3	24	0.65	7.7	69	11
Whitewater	3	9	0	0	5.8	16	0.46	7.5	53	14
Grasmere	1	6	0	0	3.4	16	0.80	7.4	83	13
Porter	2	8	0	0	4.9	19	0.65	7.5	55	9
Whatawhata										
PW2	2	9	0	0	1.1	7	0.13	7.5	109	19
PW3	2	5	0	0	1.1	4	0.10	7.4	88	20
PW5	2	9	0	0	1.3	6	0.28	7.5	107	19
Te Urewera National Park										
U8	2	19	60	100	2.3	12	0.17	7.6	199	15
U14	3	10	100	100	2.7	14	0.33	7.5	102	14
U17	2	10	60	100	3.0	11	0.36	7.3	72	12
U18	2	6	0	100	2.2	9	0.25	7.2	61	12
U21	2	6	60	100	1.8	9	0.23	7.5	80	13
U24	2	26	100	100	2.3	15	0.37	7.6	213	11

between the sites based on the physico-chemical measures above ranged from 96 to 98%.

Urewera

The 6 streams in the Urewera study were 2nd or 3rd order streams that drained into Lake Waikaremoana (Table 1). Riparian vegetation formed a canopy over the channels of all streams and was predominantly evergreen beech and / or podocarp forest. Stream substrata were mainly small and large cobbles along with some small boulders. Nutrient concentrations were moderate to low; NO_3-N ranged from 0.08-0.11 mg l^{-1} and PO_4-P ranged from 0.16-0.79 mg l^{-1}. The streams were small to medium with near-neutral pH (Table 1). Multivariate Bray-Curtis similarity between the sites based on the measures listed in Table 1 ranged fromn 83 to 95%.

Faunal characteristics (the potential colonisation pool for each stream)

Bray-Curtis similarities (presence / absence data) between baskets of substrata in each of the four Canterbury streams at the end of nine weeks colonisation were between 54 and 75%. There were 14 common taxa (those comprising 5% or more of the fauna at any time) and of these, five occurred at three of the four sites and nine occurred at all sites. At Whatawhata there were 15 common taxa and all occurred at all three sites. Bray-Curtis similarities between bricks after 6 weeks ranged between 60 and 68%. In the Urewera study, Bray-Curtis similarities on bricks collected in each stream after 15 weeks ranged from 58 to 78%. Of the 19 common taxa, 12 occurred at all sites, six at four-five sites and one at three sites.

Patterns of colonisation

Canterbury

Ordination of the basket faunas from all sites initially split the Grasmere Stream sites (Figure 1A) from the rest (stress = 0.01). Reanalysis excluding the Grasmere baskets (Figure 1B) split baskets from each of the three sites into three groups irrespective of the time they were collected (stress = 0.06). ANOSIM indicated that basket communities differed between sites (R = 0.98, P = 0.001) but not between times (R = 0.006, P = 0.47). This also held if the Grasmere baskets were excluded (R = 0.99, P = 0.001, and R = 0.04, P = 0.17, for sites and times, respectively).

Mean densities of the 13 common taxa are plotted in Figure 2. Assemblages in the baskets were clearly more similar within sites (irrespective of the time available for colonisation between disturbances) than between sites at any time. Multivariate distances between baskets colonised for the same length of time but from different sites always differed more than those from the same site, even though the latter differed in the time available for colonisation (Table 2).

Of the 90 taxa recorded during the experiment only one to four were collected in the baskets after one week of colonisation and not after nine weeks. However, they were rare species represented by only one to three individuals. Densities of the eight abundant taxa (those comprising greater than 15% of the fauna in any basket) differed most strongly between sites (Table 3). Often there were no significant differences in density with time, or there was a steady increase in density as time available for colonisation increased (Table 3).

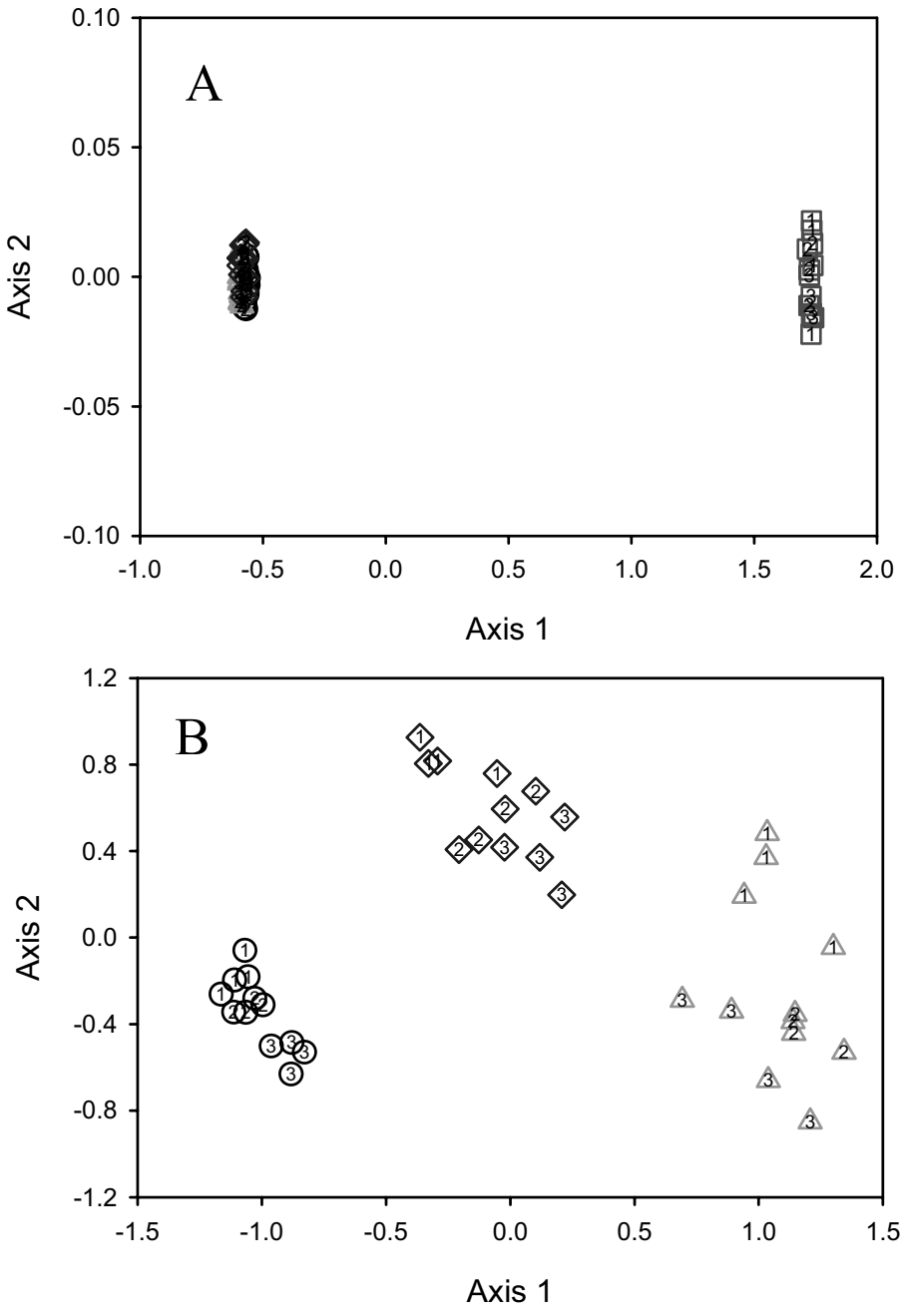

Figure 1. Plots of axes 1 and 2 of non-metric multidimensional scaling ordinations for relative abundance of invertebrates collected in A) all baskets and B) mesh baskets excluding Grasmere Stream in 4 streams [Porter River (circles), Kowai River (triangles), Whitewater Stream (diamonds) and Grasmere Stream (squares)] in Canterbury. Baskets were disturbed every week (1), every 3 weeks (2) or left undisturbed (3), before all baskets were collected after 9 weeks.

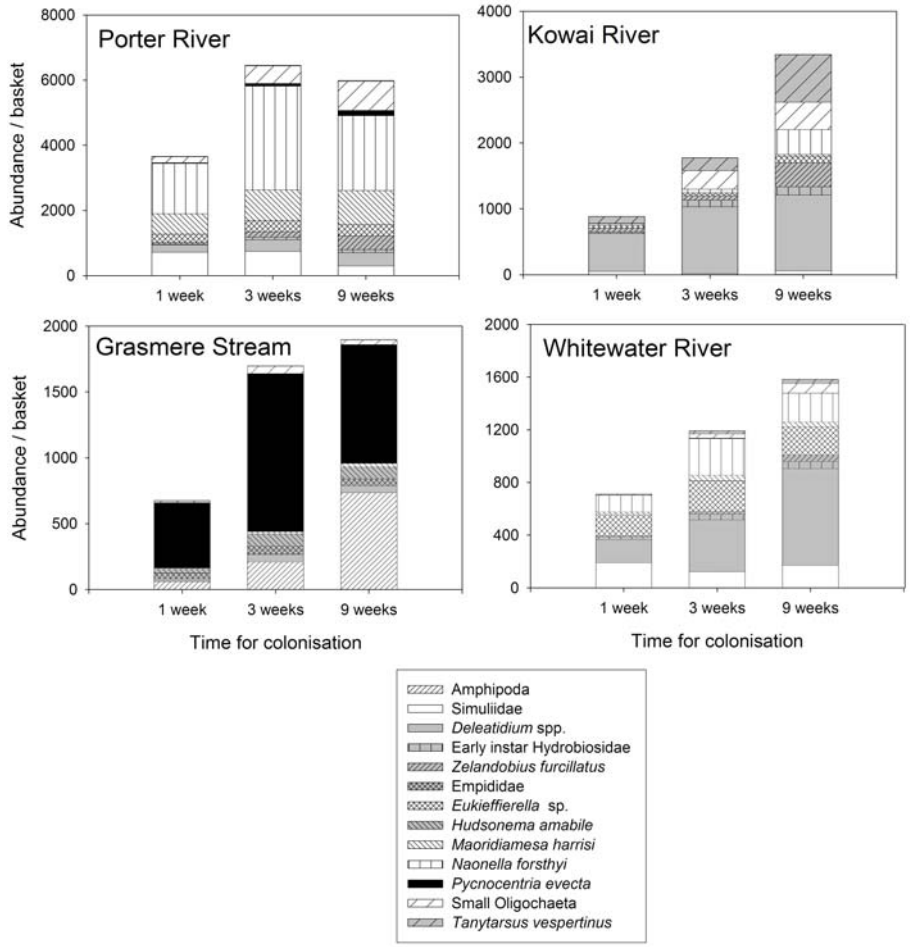

Figure 2. Mean density of common taxa (taxa comprising at least 5% of colonists at any time during the study) collected at intervals during colonisation of substrata in four Canterbury streams.

Table 2. Bray-Curtis similarity between invertebrate assemblages (mean relative abundance data) at the Canterbury sites on the first and last collection dates and compared with other sites on the first collection date.

	Same site (Week 9)	**Grasmere (Week 1)**	**Porter (Week 1)**	**Kowai (Week 1)**	**Whitewater (Week 1)**
Grasmere Stream	84.1	-	26.8	19.2	21.2
Porter River	79.7	26.8	-	46.5	46.3
Kowai River	73.1	19.2	46.5	-	54.2
Whitewater River	77.8	21.2	61.9	57.8	-

Table 3. Results of ANOVAs testing for differences in density of abundant taxa between sites and times for 4 streams in Canterbury.

	Site		Time	
	$F_{(3,42)}$	*P*	$F_{(2,42)}$	*P*
Amphipoda	222.05	<0.001	13.22	<0.001
Simuliidae	96.96	<0.001	0.74	0.48
Deleatidium spp.	185.20	<0.001	33.66	<0.001
Eukiefferiella sp.	341.14	<0.001	2.93	0.06
Maoridiamesa harrisi	96.46	<0.001	9.23	<0.001
Naonella forsythi	236.74	<0.001	5.13	0.01
Pycnocentria evecta	340.34	<0.001	12.04	<0.001
Tanytarsus vespertinus	45.97	<0.001	6.90	0.003

Whatawhata

The ordination of tile faunas from the Whatawhata streams (stress = 0.14) did not group sites together as tightly as in the Canterbury example, but there was still a closer association between tiles from the same site than for the same collection time (Figure 3). ANOSIM indicated a significant difference between faunas on tiles at different sites (R = 0.66, *P* = 0.001) but not between tiles collected at different times across sites (R = 0.14, *P* = 0.16).

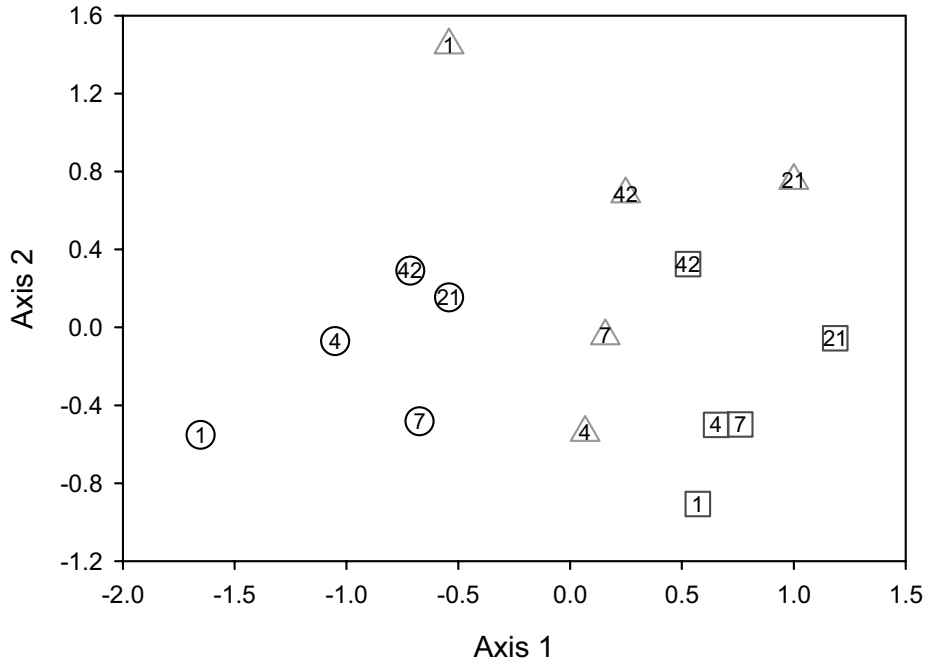

Figure 3. Plot of axes 1 and 2 of a non-metric multidimensional scaling ordination for mean relative abundance of invertebrates collected on tiles (*n*=4) on days 1, 4, 7, 21 and 42 in 3 streams at Whatawhata. Sites are PW5 (circles), PW3 (squares) and PW2 (triangles).

Plots of the mean densities of the 15 common taxa indicate much greater differences between sites than over time at the same site (Figure 4). Multivariate distances between tiles from different sites on day 1 were always more different than those between days 1 and 42 at the same site (Table 4).

Densities of the eight abundant taxa did not always differ significantly between sites or times (Table 5). However, where significant time effects occurred they were always increases in density over time (Table 5).

Of the 89 taxa collected on tiles at the Whatawhata sites only two to five were collected at a site on day 1 and were not found on day 42. However, as in Canterbury they were all rare taxa represented by one to five individuals.

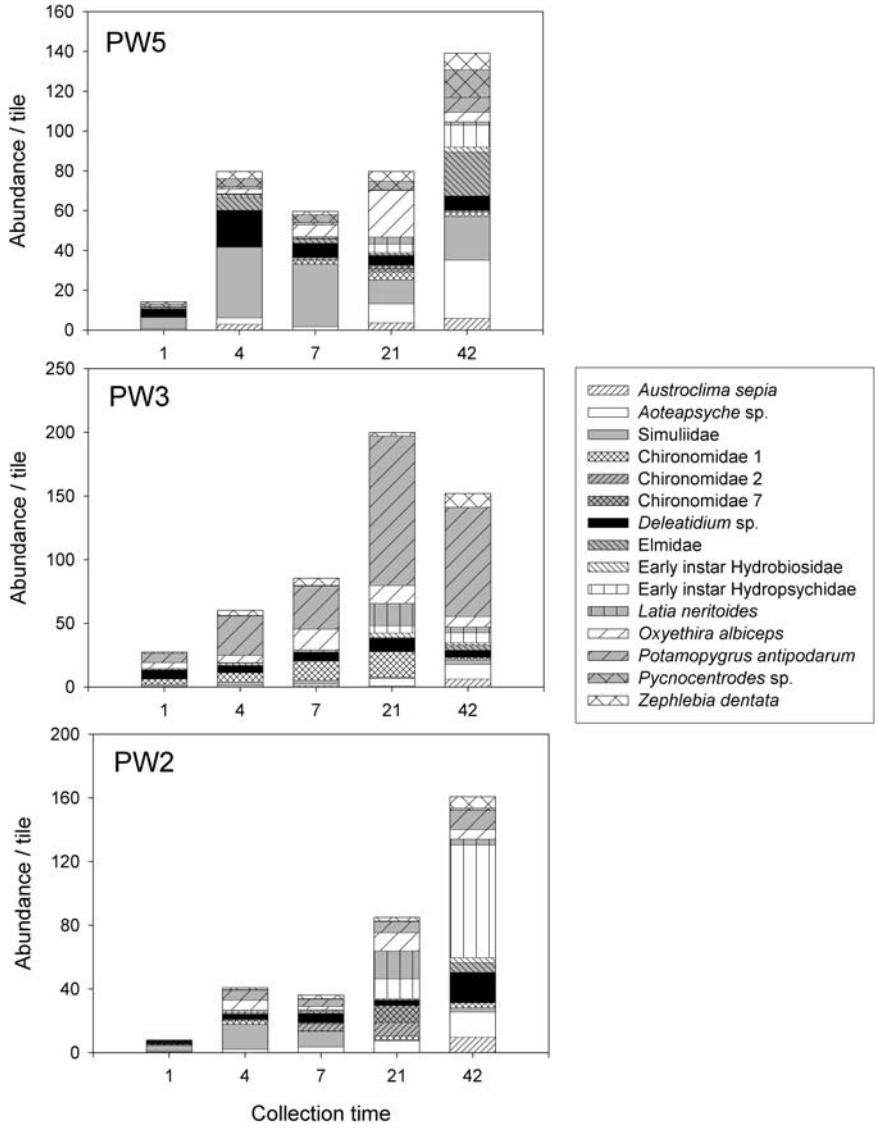

Figure 4. Mean density of common taxa (taxa comprising at least 5% of colonists at any time during the study) collected at intervals during colonisation of substrata in three Whatawhata streams.

Table 4. Bray-Curtis similarity between invertebrate assemblages (mean relative abundance data) at the Whatawhata sites on the first and last collection dates and compared with other sites on the first collection date.

	Same site (Day 42)	PW5 (Day 1)	PW3 (Day1)	PW2 (Day 1)
PW5	54.5	-	45.6	40.8
PW3	54.7	45.6	-	51.8
PW2	55.0	40.8	51.8	-

Table 5. Results of ANOVAs testing for differences in density of abundant taxa between sites and times for 3 streams at Whatawhata.

	Site		Time	
	$F_{(2, 53)}$	*P*	$F_{(5, 53)}$	*P*
Aoteapsyche sp.	6.14	0.02	58.0	<0.001
Simuliidae	15.79	<0.001	3.32	0.07
Deleatidium spp.	0.60	0.57	0.86	0.53
Chironomidae type C1	6.77	0.02	1.73	0.24
Hydropsychidae early instar	5.06	0.04	30.4	<0.001
Latia neritoides	3.68	0.07	23.8	<0.001
Oxyethira albiceps	2.91	0.11	6.23	0.01
Potamopyrgus antipodarum	34.14	<0.001	6.59	0.01

Urewera

The faunas on bricks from streams in the Urewera study were also more similar within sites (ANOSIM R = 0.76, $P = 0.001$) than within times across sites (ANOSIM R = 0.03, $P = 0.27$) (Figure 5).

Mean densities of the 19 common taxa are plotted against colonisation time in Figure 6. The sequences of arrival, and increases in density with time were markedly different among sites. Faunas in the initial stages of colonisation more closely resembled those on bricks at week 15 at the same site than those on bricks from other sites on day 3 and week 1. Bray-Curtis similarity measures (relative abundance data) between assemblages at a site on day 3 and week 15, and between a site on day 3 and other sites on day 3, indicated that in only one of 30 cases was there greater similarity between assemblages in different streams on day 3 than between assemblages in the same stream on different days (Table 6).

Analysis of variance of the densities of the six most abundant taxa indicated significant site and time differences; in general, differences between sites were considerably greater than differences between times (Table 7). All taxa except the stonefly *Zelandobius furcillatus,* which peaked in density in the middle of the experimental period, showed a steady increase in abundance with time available for colonisation. Furthermore, of the 81 collected taxa only two or three per site were collected from bricks on day 3 and week 1, and were not found in weeks 8 and 15. They were all rare species represented by only one or two individuals.

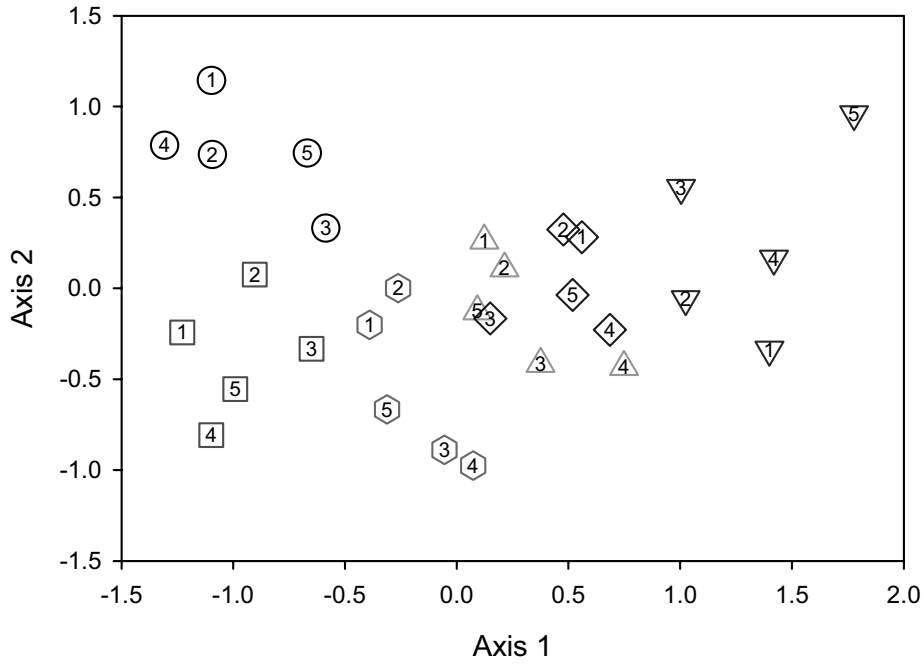

Figure 5. Plot of axes 1 and 2 of a non-metric multidimensional scaling ordination for mean relative abundance of invertebrates collected on bricks (n = 10) after 3 days (1), 1 week (2), 4 weeks (3), 8 weeks (4) and 15 weeks (5) in 6 forest streams in Te Urewera National Park. Sites symbols are shown from most to least stable indicating sites 24 (down triangle), 8 (circle), 17 (up triangle), 18 (diamond), 21 (hexagon) and 14 (square).

Table 6. Bray-Curtis similarity between invertebrate assemblages (mean relative abundance data) at Te Urewera National Park sites on the first and last collection dates and compared with other sites on the first collection date. The single bold value indicates greater similarity between collections at two different sites on the first day of collection than on the first and last dates of collection at the subject site.

	Same site (Week 15)	**Site 8 (Day 3)**	**Site 14 (Day 3)**	**Site 17 (Day 3)**	**Site 18 (Day 3)**	**Site 21 (Day 3)**	**Site 24 (Day 3)**
Site 8	59.7	-	51.1	57.2	47.5	49.5	39.8
Site 14	61.1	51.1	-	58.3	48.9	**67.5**	40.8
Site 17	73.1	57.2	58.4	-	72.1	63.6	63.8
Site 18	77.2	47.5	48.9	72.1	-	60.4	53.9
Site 21	64.5	42.6	57.0	57.4	56.3	-	45.2
Site 24	54.1	31.1	28.6	46.6	51.4	39.4	-

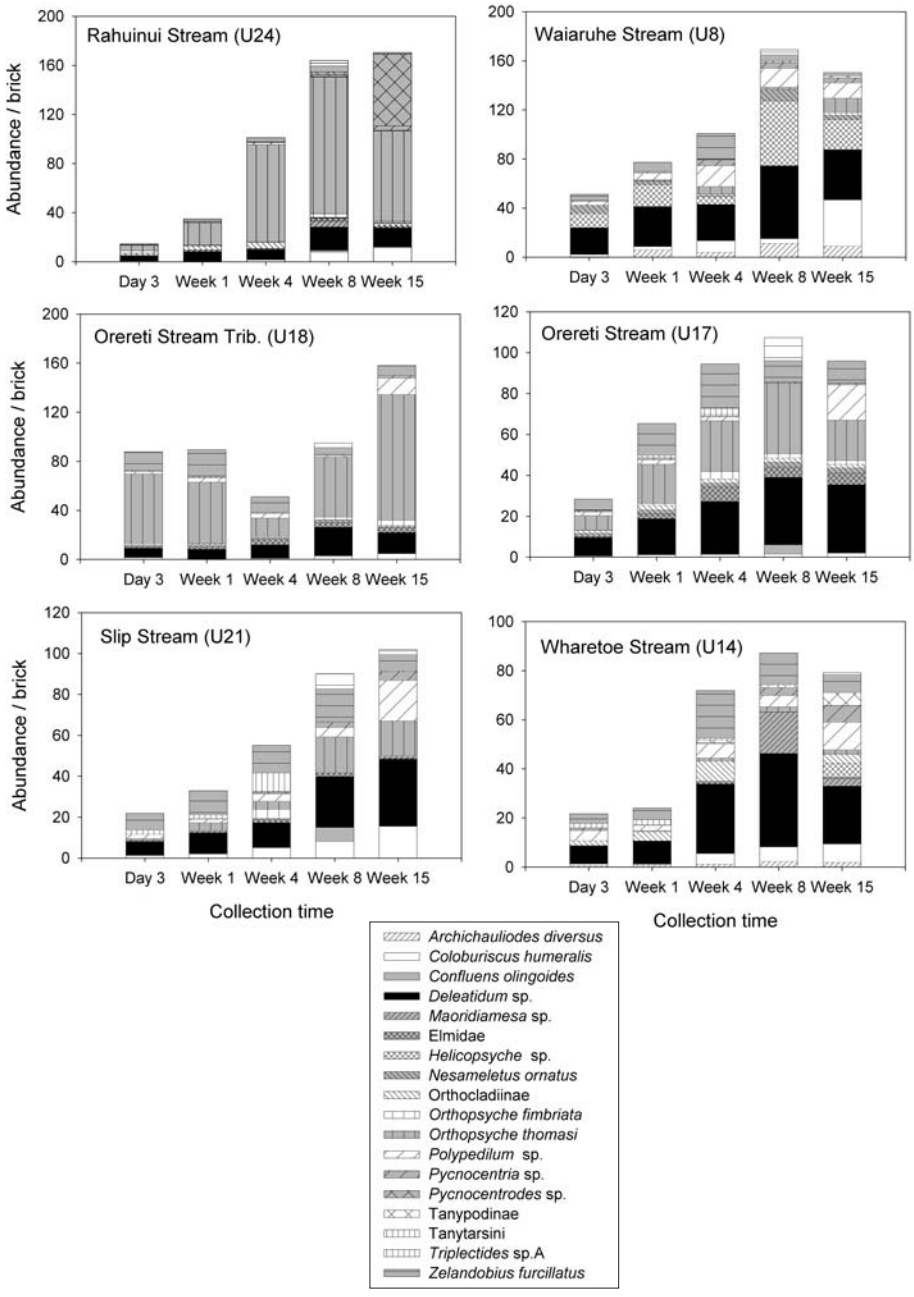

Figure 6. Mean density of common taxa (taxa comprising at least 5% of colonists at any time during the study) collected at intervals during colonisation of substrata in six forest streams in Te Urewera National Park.

Table 7. Results of ANOVAs testing for differences in density of abundant taxa between sites and times for 6 streams in Te Urewera National Park.

	Site		Time	
	$F_{(5,282)}$	*P*	$F_{(4,282)}$	*P*
Orthopsyche spp.	57.57	<0.001	24.73	<0.001
Deleatidium sp.	10.22	<0.001	15.46	<0.001
Coloburiscus humeralis	6.79	<0.001	16.48	<0.001
Helicopsyche sp.	99.04	<0.001	5.48	<0.001
Polypedilum sp.	10.15	<0.001	8.40	<0.001
Zelandobius furcillatus	15.30	<0.001	7.72	<0.001

Discussion

One of the underlying dogmas in disturbance and community ecology is that there is a suite of specialist taxa that are good colonisers but weak competitors, which arrive in a habitat soon after a disturbance, and another suite of taxa that take longer to arrive but eventually displace those colonisers through their competitive superiority (Begon *et al.* 1990; Roxburgh *et al.* 2004; Shea *et al.* 2004). However, neutral models of community structure have challenged the idea of species niche specialisation on theoretical grounds (Hubbell 2001; Chave 2004). Nevertheless, the trade-off between an organism's competitive and colonisation abilities remains a widely accepted principle that underpins such accepted phenomena in ecology as succession, as well as some more contentious concepts such as assembly rules, patch dynamics and the intermediate disturbance hypothesis (Connell 1978; Townsend 1989; Weiher & Keddy 1999). Although there are good examples of plant communities in which such trade-offs have been observed, it remains unclear how ubiquitous they are (Chesson & Huntly 1997). Furthermore, it is unclear how applicable such ideas are to communities, such as stream invertebrate assemblages, where the majority of the fauna is highly mobile (Frid & Townsend 1989; Downes 1990).

Examination of colonisation patterns in the three studies considered here revealed no evidence for the existence of taxa that could be considered early colonists of new or recently disturbed substrata and which are displaced as more taxa arrive. It could be argued that not enough time elapsed in the studies for this to occur, but the duration of the studies was similar, or greater, than that in other studies at a comparable scale in which colonisation was assumed to be complete (Lake & Doeg 1985; Mackay 1992). Furthermore, the assemblages that developed were similar to those in the surrounding stream bed, even in streams that experienced little or no disturbance. At first glance it seems that the findings are in direct contrast to the underlying assumptions discussed above, which underpin many of the ideas in modern ecology. What appears to occur is that density and diversity of taxa simply increase with time available for colonisation up to some point at which the colonisation process plateaus. As more and more individual animals discover the substrata over time, overall density increases, with corresponding increases in the density of the common organisms and

associated increases in diversity via the mechanism of passive sampling (i.e., more organisms: Magurran 2004; O'Hara 2005).

Interestingly, the fauna that colonised substrata early in the sequence in all streams more closely resembled the fauna found at the end of the sequence in the same stream than the early colonising faunas of similar, nearby streams. Therefore, at the patch scale there is no evidence of a colonisation / competition trade-off amongst individual taxa, and no evidence for the existence of a specialist suite of colonising taxa at all. The organisms that colonised newly available substrata were those that were most abundant on the streambed, and could reflect the fact that many (but not all) the streams were relatively unstable and only supported taxa that were able to recolonise quickly after spates (Death 1995; Winterbourn 1997; Death 2002, 2003). Thus, at the scale of these studies newly opened substrates were colonised by taxa drifting and walking in from nearby in roughly the same proportions as on adjacent substrata

Distinguishing whether taxa that colonise substrata in a stream do so because they are the only ones that can survive there, or because colonisation is a random process constrained only by the available species pool, is difficult. However, in each of the three examples considered in this paper the streams were very similar in habitat characteristics. Furthermore, although relative abundances of taxa might have differed between streams, almost all of the common taxa, and many of the rarer ones, could be found in all the streams within each of the studies. This indicates that most taxa could at least survive in these streams, and therefore potentially colonise the new substrata. The similarity between assemblages at a site early and late in the colonisation sequence indicates that almost all taxa were effectively colonisers, and not simply survivors.

Taxa that were abundant on substrata early in the colonisation process were Simuliidae, *Deleatidium* spp., three species of Chironomidae and *Pycnocentria evecta* (Canterbury); Simuliidae, *Deleatidium* sp., *Oxyethira albiceps* and *Potamopygrus antipodarum* (Whatawhata), and *Deleatidium* sp., *Helicopsyche* sp., *Orthopsyche* spp. and *Zelandobius furcillatus* (Urewera). Many of these taxa (or their regional equivalents) have been identified as 'good' colonisers (Mackay 1992; Death 1996), however, caddisflies and molluscs are generally considered to be taxa that are more likely to be slower colonising, competitive dominants (Hemphill & Cooper 1983; Mackay 1992; Death 1996). The abundance of crawling and drifting taxa clearly reflects the scale of the colonisation processes at play. Thus, the new patches of substrata were relatively small and reflected the scale at which bed materials are often disturbed by spates. Significantly, none of these crawling and drifting taxa declined in abundance as colonisation proceeded.

My findings need to be interpreted with some caution as the colonisation patterns found in all three studies were those associated with the disturbance of small patches of substrata within streams. It is highly likely that recovery from larger disturbances will involve different and / or additional colonisation mechanisms to those observed here, and thus could potentially conform better to ideas of colonisation / competition trade-offs discussed above. However, replicating large scale disturbances in such a way as to differentiate site- or taxon-specific

responses will be extremely difficult (but see Milner 1994). Interestingly, in one example of such a study Collier & Quinn (2003) also recorded site-specific colonisation patterns, dominated by simple accrual of individuals, rather than an identifiable assemblage of colonising taxa replaced by slower colonising competitive dominants. Unfortunately (from the perspective of the present paper), the two study sites they compared also differed in land use and riparian vegetation and it is unclear whether the site-specific responses were the result of this, or truly reflected random recolonisation processes following a large disturbance.

There are examples of competitive exclusion amongst stream invertebrate taxa (Hemphill 1988; Dudley *et al.* 1990; Kohler 1992) and of taxa that colonise newly available habitats (Pinder 1985; Downes & Lake 1991; Milner 1994). However, there is little evidence that early colonising taxa are replaced by competitively superior taxa as the latter slowly colonise, as postulated by ecological theory (but see Downes & Lake 1991; Milner 1994). In all three studies reviewed in this paper the taxa that colonised new or recently disturbed substrates were those that were dominant on the surrounding stream bed. Their colonisation therefore seemed to be a simple accumulation process brought about by their small scale movements (Ledger *et al.* 2002). Given the increasing interest in neutral models of community structure amongst the wider ecological community it might be that stream communities provide an ideal example of such models in action.

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